This Word module should be used for all taxonomic proposals.

Please complete **Part 1** and:

either **Part 3** for proposals to create new taxa or change existing taxa

or **Part 2** for proposals of a general nature.

Submit the completed Word module, together with the accompanying Excel module named in Part 3, to the appropriate ICTV Subcommittee Chair.

The Word module explains and justifies your proposal. The Excel module is a critical document that will be used to implement the proposed taxonomic changes once they are approved and ratified. If proposals presented in the Word module are not presented accurately in the Excel module, the taxonomic changes cannot proceed.

For guidance, see the notes written in blue, below, and the Help Notes in file Taxonomic\_Proposals\_Help\_2019.

**Part 1:** **TITLE, AUTHORS, etc**

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| **Code assigned:** | ***2019.005G*** |  |
| **Short title:** Create a megataxonomic framework, filling all principal taxonomic ranks, for ssDNA viruses |
|  |
| **Author(s) and email address(es):**  |
| List authors in a single line *Archives of Virology* citation format (e.g. Smith AB, Huang C-L, Santos, F) | Provide email address for each author in a single line separated by semi-colons |
| Koonin EV, Dolja VV, Krupovic M, Varsani A, Wolf YI, Yutin N, Zerbini M, Kuhn JH | koonin@ncbi.nlm.nih.gov; doljav@science.oregonstate.edu; mart.krupovic@pasteur.fr; Arvind.Varsani@asu.edu; wolf@ncbi.nlm.nih.gov; yutin@ncbi.nlm.nih.gov; zerbini@ufv.br; kuhnjens@mail.nih.gov  |
| **Corresponding authors** |
| Koonin, Eugene V.; koonin@ncbi.nlm.nih.govKuhn, Jens H.; kuhnjens@mail.nih.gov |
| **List the ICTV study group(s) that have seen this proposal:** |
| A list of study groups and contacts is provided at <http://www.ictvonline.org/subcommittees.asp> . If in doubt, contact the appropriate subcommittee chair (there are six virus subcommittees: animal DNA and retroviruses, animal ssRNA-, animal ssRNA+, fungal and protist, plant, bacterial and archaeal) | **ICTV *Bacilladnaviridae, Bidnaviridae*, *Circoviridae, Geminiviridae, Genomoviridae, Inoviridae*, *Microviridae*, *Nanoviridae*, *Parvoviridae*, *Polyomaviridae*, *Papillomaviridae*, and *Smacoviridae* Study Group Chairs; ICTV Bacterial and Archaeal Viruses Subcommittee; ICTV Animal dsRNA and ssRNA- Viruses Subcommittee Chair; ICTV Animal DNA Viruses and Retroviruses Subcommittee Chair; ICTV Plant Viruses Subcommittee Chair; ICTV Fungal and Protist Viruses Subcommittee Chair****This is a direct submission to the entire ICTV Executive Committee** |
| **ICTV Study Group/Author comments (if any) and response of the proposer:** |
| Here we propose a megataxonomic framework for single-stranded DNA (ssDNA) viruses by assigning ICTV-ratified taxa (i.e., species, genera, subfamilies, and families) to available, but presently unfilled major megataxonomic ranks (orders, classes, phyla, and kingdoms). The goal of this proposal is to provide taxonomic “buckets” or “place holders” that enable ICTV Study Groups to accommodate the close-to-exponentially increasing number of novel viruses that are related to, but distinct from, viruses that constitute the already established taxa. The awareness of these novel viruses often goes hand-in-hand with the realization that current orders might have to be promoted to orders (e.g., *Inoviridae*) or that entire family structures need to be completely re-evaluated (e.g., *Papillomaviridae*). We surmise that the absence of established higher taxa and the absence of ICTV Study Groups for such taxa may have had an adverse effect, leading to large groups of classifiable viruses not becoming classified. Vice versa, placing currently established taxa together into higher-rank taxa may initiate long-overdue, likely intense, discussions between currently non-interacting ICTV Study Groups to examine higher-rank evolutionary relationships of the viruses they are engaged with. The megataxonomy outlined in this proposal is to be seen only as an initial step and we fully expect this framework to change substantially over time.We:* aim to bring virus taxonomy into better accordance with other biological taxonomies, which require novel organisms to be classified into all available principle/primary ranks even if this means that certain higher-ranked taxa only include single lower-ranked taxa. For instance, in animal taxonomy, the unranked supergroup Hemimastigophora includes a single class Hemimastigidea, which includes a single order Hemimastigida, which includes a single family Spironem(atelli)idae (which includes 4 genera). Likewise, in prokaryotic taxonomy, the bacterial species *Elusimicrobium minutum* is the only included species in genus *Elusimicrobium*, which is the only genus in family *Elusimicrobiaceae*, which is the only family in order *Elusimicrobiales*—that order is the only order in class *Elusimicrobia*, which is the only class in phylum *Elusimicrobia*. Obviously, taxon demarcation criteria cannot be established for single taxon-including higher-ranked taxa and hence their definitions are identical to those of the higher-ranked taxa for the time being, i.e., until the discovery of novel organisms requires the creation of sister taxa. However, filling all principle ranks provides a sense of “scaling”, i.e. a current assessment of how distant a particular organism is from other classified taxa; this “scaling” argument was used successfully previously in TaxoProps establishing the availability of taxonomic ranks above order and the establishment realm *Riboviria*;
* deliberately propose the creation of higher-ranked taxa that currently include only single lower-ranked taxa, either because we are aware from the literature that an existing lower-rank taxon will have to be promoted to a higher rank in the near future due to overbearing virus diversity or because we are aware from the literature of large virus groups for which higher-rank taxa will have to be established shortly; we hope that the created higher-ranked taxa will provide an impetus for the community to classify already known highly divergent virus groups;
* deliberately did not fill any secondary (sub-)ranks as the filling of such ranks is not mandatory in other biological taxonomies;
* deliberately focus this proposal only on official taxa (rather than, for instance, proposing novel species that could become the founding members of “obvious” novel higher-rank taxa we are certain will need to be established) to keep this proposal relatively simple;
* emphasize that, although we posit that our rationale for creating a megataxonomy is sufficient, this rationale can, such a focus must be seen as a rough guide for lower-rank taxonomy, so that other methods (e.g., sequence-based methods such as GRAViTy, pairwise genome sequence comparisons, phylogenies of individual ORFs or proteins; structural comparisons of encoded proteins or virions; phenotypic virus characteristics) will have to be used to resolve lower-rank relationships and likely to refine higher-rank relationships.
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|  |
| Date first submitted to ICTV: | June 19, 2019 |
| Date of this revision (if different to above): | October 18, 2019 |

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| --- |
| **ICTV-EC comments and response of the proposer:** |
| Per the minutes of the last ICTV Executive Committee meeting (EC51, July 15–17, 2019, Berlin, Germany), the EC voted for minor revisions of this proposal (Uc) with 17/19 votes in favor. The EC asked for the following steps to be taken prior to submission of this revision:1. Consult all affected Study Group once again for feedback

Response: all relevant Study Group Chairs were contacted for a second time and asked to provide input and criticisms. None of the Study Groups disagreed with the overall taxonomic proposal, i.e., the proposed relationship between officially established taxa. Concerns were voiced about certain proposed taxon names and the Study Groups’ suggestion were mostly followed and names were changed accordingly for this revision.1. Provide any feedback from Study Groups to the ICTV President

Response: all relevant Study Group responses (and all TaxoProp author rebuttals or explanations) were forwarded to the ICTV President and the ICTV Executive Committee per email.1. Regarding proposed taxon names using people’s names, provide permissions from these people (if alive) to use their names to the ICTV President and the ICTV Proposals Secretary

Response: all relevant permissions were forwarded to the ICTV President, the ICTV Proposal Secretary, and the ICTV Executive Committee per email. |

**Part 3:** **PROPOSED TAXONOMY**

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| **Name of accompanying Excel module:** 2019.005G.A.v1.Monodnaviria.xlsx |

**INTRODUCTION**

Recent advances of comparative genomics and metagenomics uncover a close-to-exponentially increasing number of diverse viruses. These discoveries not only vastly improve our understanding of the evolutionary relationships within the virosphere, but also emphasize that the existing taxonomic framework is inadequate to depict the relationships within the virosphere. The currently available dataset of virus genome sequences and increasingly sophisticated methods for analysis beyond “simple” phylogenies (e.g., gene network analysis, iterative and self-optimizing sequence alignments) enable us now to roughly outline the global organization of the virus world in its entirety, including key evolutionary events that resulted in the emergence of major virus clades.

Depicting the evolutionary relationships among viruses necessarily depends on the identification of hallmark genes/proteins that connect them. In contrast to cellular organisms, such hallmark genes are not universally shared among all viruses [[9](#_ENREF_9)] and it is therefore currently presumed that viruses have several distinct points of origin, i.e., that they cannot be united under a single highest taxon rank on evolutionary grounds. Nevertheless, extensive analyses of the evolution of large groups of viruses, rather than all of them, have proved productive. The primary approach taken in such studies is the phylogenetic analysis of genes that are conserved across those groups, known as Virus Hallmark Genes (VHGs), which are responsible for the key functions in virus replication and virion morphogenesis [[9](#_ENREF_9)]. The most widely spread VHGs are:

* RNA-directed RNA polymerases (RdRps);
* RNA-directed DNA polymerases/reverse transcriptases (RTs) that are homologous to RdRPs;
* superfamily 3 helicases (S3Hs);
* single jelly-roll major capsid proteins (SJR-MCPs);
* double jelly-roll major capsid proteins (DJR-MCPs); and
* rolling-circle replication initiation endonucleases (RCREs) [[9](#_ENREF_9), [11](#_ENREF_11), [12](#_ENREF_12)].

Using these VHGs, megataxonomic scaffolds can be established that are further informed, if necessary, by dissection of bipartite gene-genome networks of viruses into distinct modules [[4-6](#_ENREF_4), [10](#_ENREF_10), [21](#_ENREF_21)]. These analyses indicate that a substantial majority of currently classified viruses can be assigned to one of four, likely, evolutionarily independent virus realms. Because the International Committee on Taxonomy of Viruses (ICTV) has recently formally approved creation of taxa above the rank of order, the door is now open to formalize the megataxonomic scaffolds that resulted from VHG analyses within the official ICTV-supported taxonomy.

Here we propose a megataxonomic structure for one of these groups: ssDNA viruses.

**MEGATAXONOMY OF ssDNA VIRUSES**

Single-stranded DNA (ssDNA) viruses are highly diverse and abundant in different habitats [[5](#_ENREF_5), [18](#_ENREF_18), [20](#_ENREF_20), [25](#_ENREF_25), [26](#_ENREF_26), [28](#_ENREF_28)]. The ssDNA viruses are currently classified into four families of prokaryotic viruses (*Inoviridae*, *Microviridae*, *Pleolipoviridae* and *Spiraviridae*), and nine families of eukaryotic viruses (*Anelloviridae*, *Bacilladnaviridae, Bidnaviridae*, *Circoviridae*, *Geminiviridae*, *Genomoviridae*, *Nanoviridae*, *Parvoviridae* and *Smacoviridae*). Most ssDNA viruses have small circular genomes that replicate via the rolling circle mechanism [[33](#_ENREF_33)]. The ssDNA viruses with circular genomes that encode a replication initiator protein (Rep), i.e., those classified in the families *Bacilladnaviridae*, *Circoviridae*, *Geminiviridae*, *Genomoviridae*, *Inoviridae*, *Microviridae*, *Nanoviridae*, *Pleolipoviridae* and *Smacoviridae*, and many more unclassified viruses, have been collectively referred to as circular Rep-encoding single-strand (CRESS)-DNA viruses [[24](#_ENREF_24), [32](#_ENREF_32), [33](#_ENREF_33)]*.* Parvovirids and bidnavirids have linear ssDNA genomes [[4](#_ENREF_4), [15](#_ENREF_15)]. Parvovirids replicate via a rolling hairpin mechanism [[31](#_ENREF_31)], whereas bidnavirids encode their own protein-primed family B DNA polymerases [[15](#_ENREF_15)]. Notably, different pleolipovirids encapsidate either ssDNA or dsDNA genomes [[1](#_ENREF_1), [23](#_ENREF_23)].

With the exception of anellovirids, bidnavirids, spiravirids, and certain inovirids, all ssDNA virus genomes encode so-called His-hydrophobic-His (HUH) endonuclease domains that cleave genomic DNA at specific sites and initiate rolling circle (or rolling hairpin) replication [[2](#_ENREF_2), [8](#_ENREF_8)]. All eukaryotic CRESS-DNA viruses also encode superfamily 3 helicases (S3Hs) that most often are fused to HUH endonucleases to form the two-domain Reps; in contrast, prokaryotic ssDNA viruses encode solitary HUH endonucleases [[6](#_ENREF_6), [10](#_ENREF_10), [13](#_ENREF_13)]. Apart from inovirids, pleolipovirids, spirovirids, and the recently discovered *Flavobacterium*-infecting, lipid-containing phage (FLiP) that is expected to form a new family *Finnlakeviridae* [[17](#_ENREF_17)],ssDNA viruses have capsids made of single jelly roll (SJR) major capsid proteins (MCPs).

Sequence comparison and phylogenetic analyses of HUH endonucleases, S3Hs, and CPs of ssDNA viruses indicate multiple, chimeric origins of these viruses [[10-14](#_ENREF_10), [27](#_ENREF_27)]. The CRESS-DNA virus Reps are most closely related to the homologous Reps of small, rolling circle-replicating bacterial plasmids that also consist of HUH and S3H domain-encoding genes. Moreover, phylogenetic analysis of Reps shows that the replication machinery of CRESS-DNA viruses evolved from that of plasmids on at least three independent occasions [[10](#_ENREF_10)]. Similarly, HUH endonucleases of prokaryotic CRESS-DNA viruses seem to have originated from plasmid endonucleases that are not fused to S3Hs. The CPs of eukaryotic CRESS-DNA viruses appear to originate from a completely different source: these proteins are most closely related to the CPs of different groups of plant and animal (+)RNA viruses. Thus, eukaryotic CRESS-DNA viruses apparently evolved on multiple, independent occasions via the same route, namely, recombination between a bacterial plasmid and a cDNA copy of a (+)RNA virus. The realization of this scenario in the evolution of multiple groups of CRESS-DNA viruses appears to be one of the most striking examples of large-scale convergent evolution in the virus world and beyond. The provenance of the divergent microvirid SJR-CPs remains uncertain [[16](#_ENREF_16)].

Phylogenetic analysis of Reps reveals two large groups of eukaryotic CRESS-DNA viruses, each including several families/clades, which could be united in a higher ranked taxon, whereas all CRESS-DNA viruses could be unified at an even higher rank [[10](#_ENREF_10)]. The CRESS-DNA viruses (proposed phylum *Cressdnaviricota*) apparently gave rise to parvovirids, with their linear ssDNA genomes. Remarkably, small dsDNA viruses with circular genomes, members of the families *Papillomaviridae* and *Polyomaviridae* (joined together in a new class *Papovaviricetes*), appear to have evolved from ssDNA viruses, most likely, parvovirids, via a major transition that involved inactivation of the HUH domain of the Rep that became a DNA-binding domain [[9](#_ENREF_9)]. Concomitantly, the replication mode of these viruses switched from the rolling circle mechanism to the “theta” bidirectional mechanism resembling plasmid and bacterial chromosome replication. The CPs of small dsDNA viruses are highly divergent, so it remains unclear whether these CPs evolved from parvovirus CPs or were recruited independently [[16](#_ENREF_16)]. Consequently, parvovirids and papillomavirids/polyomavirids could join the assemblage of CRESS-DNA viruses at a top taxonomic rank (proposed kingdom *Shotokuvirae*).

 Phylogenomic analysis of ssDNA viruses strongly supports their polyphyly. Nevertheless, the close similarity of the genome structure and length as well as the gene compositions of these viruses justify the creation of a realm to encompass them all. This proposal is to be considered as an operational move to formalize an obvious relationship between the mentioned ssDNA viruses based on common VHGs.

**Taxon demarcation criteria:**

The International Code of Virus Classification and Nomenclature (ICVCN) is currently ambiguous regarding the need for taxon demarcation criteria at higher ranks. Three Rules appear to be applicable (emphasis in italics is ours):

“3.5 Taxa will be established only when representative member viruses are sufficiently well characterized and described in the published literature so as to allow them to be identified unambiguously *and the taxon to be distinguished from other similar taxa*”;

“3.22 Every individual virus is a physical entity and treated as belonging to a number of taxa of hierarchical ranks, *some of which may remain undefined*”;

and

“3.24 The classification of a virus at the species and genus ranks is mandatory. *Classification may also encompass any further number of taxa at higher hierarchical ranks*”

Because our proposal only encompasses already established taxa, all viruses affected by our proposal have been “sufficiently well characterized” as otherwise they would not have been classified into these established taxa in the first place. Furthermore, Rule 3.22 permits establishing ranks that for the moment remain undefined; and Rule 3.24 indicates no restriction of ranks to be established.

Nevertheless, for the time being, we suggest the following provisional taxon demarcation criteria while being aware that these may have to be revisited whenever new members of the realm are being proposed:

1. *Monodnaviria*: a virus is a member of this realm if it has a ssDNA genome encoding a rolling-circle replication endonuclease of the HUH superfamily or if it is derived from such a virus
2. *Loebvirae*: a *Monodnaviria* member is a member of the included kingdom *Loebvirae* if it infects prokaryotes, but not eukaryotes, has a filamentous or rod-shaped virion formed from an alpha-helical capsid protein and encodes a characteristic morphogenesis protein, an ATPase of the FtsK-HerA superfamily
3. *Sangervirae*: a *Monodnaviria* member is a member of the included kingdom *Sangervirae* if it infects prokaryotes, but not eukaryotes, and has a single jelly-roll capsid protein and a characteristic pilot protein required for DNA transfer across cell envelope; thus far, the Rep proteins in this kingdom appear to be monophyletic and could be used as an additional unifying feature
4. *Shotokuvirae*: a *Monodnaviria* member is a member of the included kingdom *Shotokuvirae* if it encodes a characteristic Rep protein containing an N-terminal endonuclease domain (or derivative thereof) and a C-terminal superfamily 3 helicase domain. This kingdom also includes derivatives of bona fide members (e.g., class *Mouviricetes*)
5. *Cossaviricota*: a *Shotokuvirae* member is a member of the included phylum *Cossaviricota* if it is not a member of phylum *Cressdnaviricota* (see TaxoProp TaxoProp2019.012 by Krupovic *et al*.)
6. *Trapavirae*: a *Monodnaviria* member is a member of the included kingdom *Trapavirae* if it infects prokaryotes, but not eukaryotes, and has an enveloped virion containing a characteristic membrane fusion protein, exemplified by VP5 of Halorubrum pleomorphic virus 2.

If a principle rank taxon includes only a single lower-ranked taxon, then the definition of the lower-ranked taxon is, for now, identical to the definition of the higher-ranked taxon.

Truly useful taxon demarcation criteria will have to be established in the future, likely by incorporating yet-unclassified virus groups into the realm.

**Etymology of proposed taxa:**

* *Monodnaviria*; from Greek μόνος [mónos], meaning single (a reference to single-stranded DNA) and DNA; and the suffix -*viria* for realm taxa
* *Loebvirae*; after T. Loeb†, who described “phage f1” in 1960 [[19](#_ENREF_19)]; and the suffix -*virae* for kingdom taxa
* *Hofneiviricota*; after Peter H. Hofschneider†, who described “phage M13” in 1963 [[7](#_ENREF_7)]; and the suffix -*viricota* for phylum taxa
* *Faserviricetes*; after German Faser, meaning fiber (a reference to *Inoviridae*, which is derived from Greek ίνα [ína]); and the suffix -*viricetes* for class taxa
* *Tubulavirales*; from tubular, a reference to the virion morphology of some viruses in this taxon; and the suffix -*virales* for order taxa
* *Sangervirae*; after Frederick Sanger†, who used “phage ΦX174” to determine the first-ever DNA genome sequence [[29](#_ENREF_29)]; and the suffix -*virae* for kingdom taxa
* *Phixviricota*; a portmanteau of “phage ΦX174”; and the suffix -*viricota* for phylum taxa
* *Malgrandaviricetes*; after Esperanto malgranda, meaning micro/small; and the suffix -*viricetes* for class taxa
* *Petitvirales*; from French petit, meaning small (micro); and the suffix -*virales* for order taxa
* *Shotokuvirae*; after Japanese Empress Shōtoku (称徳天皇), aka Kōken (孝謙天皇)†, who wrote a poem about a plant disease highly likely caused by a geminivirus—likely the first written record of a plant virus disease and a disease caused by a CRESS-DNA virus [[30](#_ENREF_30)]; and the suffix -*virae* for kingdom taxa
* *Cossaviricota*; after Yvonne Cossart†, who co-discovered parvovirus B19 [[3](#_ENREF_3)]; and the suffix -*viricota* for phylum taxa
* *Quintoviricetes*; after Galician quinto, meaning fifth (a reference to Fifth disease, a disease caused by parvovirus B19); and the suffix -*viricetes* for class taxa
* *Piccovirales*; from Italian piccolo, meaning small (parvus); and the suffix -*virales* for order taxa
* *Mouviricetes*; after French mou, meaning flaccid (flacher); and the suffix -*viricetes* for class taxa
* *Polivirales*; a portmanteau of polinton-like virus; and the suffix -*virales* for order taxa
* *Papovaviricetes*; reinstating word stem papova (former “*Papovaviridae*”, which included both polyomaviruses and papillomaviruses); and the suffix -*viricetes* for class taxa
* *Sepolyvirales*; after SE [Stewart & Eddy] polyoma, the first designation for the first discovered polyomavirus (now murine polyomavirus); and the suffix -*virales* for order taxa
* *Zurhausenvirales*; to honor Harald zur Hausen, who discovered the connection of papillomaviruses and cervical cancer; and the suffix -*virales* for order taxa
* *Trapavirae*; after Trapani, Italy, where Halorubrum pleomorphic virus 1 (HRPV-1, member of the type species of *Alphapleolipovirus*, *Pleolipoviridae*) was discovered [[21](#_ENREF_21)], and the suffix -*virae* for kingdom taxa
* *Saleviricota*; after Italian sale, meaning salt—a reference to the halophilic hosts of most pleolipovirids; and the suffix -*viricota* for phylum taxa
* *Huolimaviricetes*; after Finnish huolimaton, meaning sloppy—a reference to the “sloppy” assembly of pleolipovirions [[22](#_ENREF_22)]; and the suffix -*viricetes* for class taxa
* *Haloruvirales*; after Halorubrum pleomorphic virus 1 (HRPV-1, member of the type species of *Alphapleolipovirus*, *Pleolipoviridae*); and the suffix -*virales* for order taxa

One of the proposed taxon names, *Zurhausenvirales,* is derived from the name of a living person. The permission of this person to use his name has been forwarded to the ICTV Executive Committee.

**List of official (ss and ds) DNA virus taxa that we propose remain unassigned to any realm, including the one proposed here, until further data become available:**

* *Anelloviridae*
* *Ampullaviridae*
* *Baculoviridae*
* *Bicaudaviridae*
* *Clavaviridae*
* *Dinodnavirus*
* *Finnlakeviridae* [proposed]
* *Fuselloviridae*
* *Globuloviridae*
* *Guttaviridae*
* *Halspiviridae* [proposed] including *Salterprovirus*
* *Hytrosaviridae*
* *Ligamenvirales*
* *Nimaviridae*
* *Nudiviridae*
* *Ovaliviridae*
* *Plasmaviridae*
* *Polydnaviridae*
* *Portogloboviridae*
* *Rhizidiovirus*
* *Spiraviridae*
* *Thaspiviridae* [proposed]
* *Tristromaviridae*

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| --- |
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